4. CLASSIFICATION OF HABITATS BY SELECTION PRESSURES: A SYNTHESIS OF LIFE-CYCLE AND r/K THEORY

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SUMMARY

High offspring survivorship selects for greater reproductive investment: towards semelparity (breed once then die) as opposed to iteroparity (repeated breeding). Better growth conditions for juveniles selects for the production of more smaller offspring, as opposed to fewer larger offspring. These predictions form the basis of a classification of habitats in terms of indices S and G related to offspring survivorship and growth conditions respectively. This classification is discussed in relation to the r–K and other classifications.

INTRODUCTION

Much attention has been given to the problem of classifying habitats according to selection pressures, in the hope of being able to associate the characteristics of habitats with those of the organisms found within them. This was the basis of much of the early work on comparative ecophysiology (e.g. Chapman 1931). As evolutionary and ecological theory has matured, however, there has been a welcome shift in this programme from a posteriori description to a priori prediction (Calow & Townsend 1981) and from a concern with the particular, to the development of a general classification, the dream of an 'ecological periodic table' (Southwood 1977).

Perhaps the first rigorous attempt at such a predictive general classification was the r/K dichotomy of MacArthur (particularly well presented in MacArthur 1972). In its most basic form this is concerned with the *effects of population density* on general demographic traits (Boyce, in press), especially on fitness, F, measured by rate of increase per individual. The simplest possible relation between this measure of fitness and density is the straight line

$$\text{(rate of increase per individual)} = r - r/K \text{ (density)},$$

where r and K are parameters characterized below. Writing density $= N$ gives

$$\frac{1}{N}\frac{dN}{dt} = r - \frac{r}{K}N \tag{1}$$

$$\therefore \frac{dN}{dt} = N\left(r - \frac{rN}{K}\right) \tag{2}$$

which provides the starting point for contemporary population dynamics. Rate of increase per individual is a measure of fitness (F) of an organism obtained by (simplistically) ignoring all age structure. Much confusion arises because intrinsic rate of increase has been used in two different senses, both to mean $1/N\ dN/dt$, i.e. fitness, and to mean fitness at zero density, i.e. r_A or r_B in Fig. 4.1. The phrase 'intrinsic rate of increase' will therefore be abandoned in this paper.

Characters bringing about high F at low density might be the same as those bringing about high F at high density, in which case there is no more to say. On the other hand, if superior fitness at low density is incompatible with superior fitness at high density, then two distinct types of organisms may evolve; A being fitter than B at low density and B being fitter than A at high density. In Fig. 4.1, rate of increase per individual at zero density is labelled r, and density when rate of increase per individual is zero is labelled K (carrying capacity). A increases at a faster rate at low density ($r_A > r_B$) and is said to be r-selected. On the other hand, B increases at a faster rate at high density provided its carrying

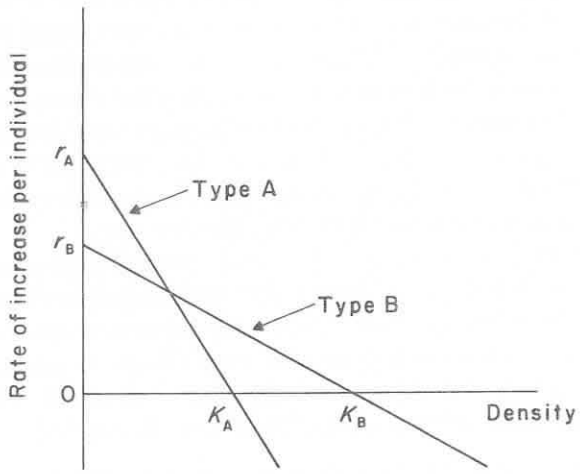

FIG. 4.1. r- and K-selection (see text for explanation). (After MacArthur, 1972.)

capacity is higher ($K_B > K_A$) (MacArthur 1972; Sibly & Calow 1983), and B is said to be *K*-selected.

However, a classification of selection pressures based only on the effects of density N on fitness F cannot be very precise because F is made up of a number of components (fecundity, survivorship, growth rate of offspring; see below), different values of which might maximize F at either low or high density. Moreover, the density effects themselves might occur in different ways (e.g. as a result of competition, predation or dispersal) and the consequences of one might not be the same as those of another (Boyce, in press). Only by the addition of a number of auxiliary hypotheses has it been possible to construct classifications rich with predictions about phenotypic traits. Thus, the 'Principle of Allocation', that organisms with finite resources have to allocate them between competing metabolic demands, ensures a trade-off between fecundity-promoting and survival-promoting traits (Cody 1966; see also Calow 1979) and the suggestion of an incompatibility between high rates and high efficiencies of production also predicts precise distinctions between traits that should evolve under conditions with and without resource limitations (Odum & Pinkerton 1955; MacArthur 1972; Smith 1976). Pianka (1970) seems to have made a number of implicit assumptions in constructing his detailed catalogue of differences between the consequences of r and K selection (e.g. his Table 1). Recognizing the limitations of a classification based on a single parameter, population density, other authors have tried to enrich the theory by incorporating other forces. Whittaker (1975), for example, pointed out that some populations occur in harsh environments and that environmental stress might have been a dominant force in shaping their evolution. Environmental stress is also incorporated into the classificatory schemes of Grime (1974, 1979), Southwood (1977) and Greenslade (1983).

The problem with such developments is not so much that they are outwith the spirit of what MacArthur intended (Boyce, in press), but that they are not defined very rigorously. However, rigorous definition is now made feasible by parallel developments in an appreciation of the way F is affected by age-specific schedules of survivorship, fecundity and growth rate of offspring (life-cycle or life-history theory; Charlesworth 1980; Sibly & Calow 1983). The intention here is to use life-history theory to construct an enlarged, but rigorous, classification of selection pressures, based on Pianka's classification since this has had an enormous influence on the development of research in evolutionary ecology.

We will conclude that one-dimensional classification, by population density, should be replaced by a two-dimensional scheme in which the classifying variables are those identified as being of key importance in life-cycle evolution. The two variables are: (i) an index of age-specific

survivorship (S) and (ii) an index of growth rate of offspring (G). Both S and G are determined by environmental conditions (extrinsic factors) but are influenced by internal constraints and trade-offs (intrinsic factors). By definition, habitat classification is more concerned with extrinsic factors, but in practice extrinsic and intrinsic factors are often difficult to distinguish. Therefore, after defining S and G in terms of life-cycle theory we offer operational definitions as the first stage towards applying the classification in the real world. Finally, we also discuss how the classification, based on S and G, relates to the ones of Whittaker, Grime and Greenslade mentioned above.

Pianka's predictions

From the point of view of this paper, there are two main predictions about life-cycle traits in Pianka's classification (Pianka 1970).

1 At higher population densities, with more competition, the optimal strategy is to allocate less matter and energy to reproduction, and more to adult maintenance.

2 At higher population densities, with more competition, the optimal strategy is to produce fewer, larger offspring.

These will be referred to as predictions 1 and 2. They deal with the questions of how much to invest in reproduction, and how to distribute that investment between individual offspring. We shall use life-cycle theory to evaluate predictions 1 and 2, and put forward two new predictions (3 and 4) after defining fitness and hence identifying the fundamental basis of the theory.

Definition of fitness

As stated above the fitness F of phenotype p in environment E is measured as its rate of increase per individual, and is defined by the equation

$$1 = \sum_t e^{-Ft} l_t(\mathrm{p,E}) n_t(\mathrm{p,E}) \qquad (3)$$

where t is age in years, $l_t(\mathrm{p,E})$ is survivorship from birth until age t of females of phenotype p in environment E, and $n_t(\mathrm{p,E})$ is the number of female offspring produced per breeding female of age t with phenotype p in environment E. If the sexes have different life histories a more sophisticated approach must be used (for further discussion see Charlesworth 1980, and Bulmer 1983). If we assume that age and experience have no effect on adult rates of survival and reproduction, so that the number of female offspring produced per female is always n, then eqn (3) can be simplified. The form it takes depends on whether the costs of reproduction are incurred before the

eggs are laid (here referred to as *direct costing*) or after the eggs are laid (*absorption costing*) (Sibly & Calow, in press). Costs of reproduction are in terms of increased adult mortality or increased delay before breeding again. Under direct costing eqn (3) simplifies to

$$1 = e^{-(F+\mu_1)t_1}n + e^{(F+\mu_2)t_2} \tag{4}$$

where μ_1 is juvenile mortality rate from birth to maturity (defined as the moment when costs of reproduction are first paid) at age t_1, μ_2 is adult mortality rate, and time t_2 elapses between maturity and breeding, successive breedings also being at intervals t_2 apart. It will sometimes be convenient to replace $e^{-\mu_1 t_1}$ by S_1 (juvenile survivorship) and $e^{-\mu_2 t_2}$ by S_2 (adult survivorship between breedings). Under absorption costing eqn (3) simplifies to

$$1 = e^{-(F+\mu_1)t_1}n + e^{-(F+\mu_2)t_2} \tag{5}$$

with the same notation except that first breeding occurs at maturity; successive breedings are still intervals t_2 apart.

LIFE-CYCLE THEORY AND PIANKA'S PREDICTIONS

Prediction 1

Prediction 1 was that at lower density with less competition the optimal strategy would be to put more matter and energy into reproduction each breeding season. Thus, if initial offspring size is constant, more offspring will be obtained (the trade-off between offspring number and initial offspring size will be considered in the next section). Increased investment in offspring will however be at some cost to the adult, and it will be assumed here that the cost is increased adult mortality (though it could in principle be in terms of increased time between breeding, see Sibly & Calow 1983, for a discussion). In both direct and absorption costing a trade-off is thought to exist between offspring number and adult mortality, since resources devoted to reproduction (increasing n) are denied to body maintenance (increasing μ_2), a trade-off which probably occurs generally (Williams 1966; Calow & Sibly 1983; Sibly & Calow 1983 and in press; Calow 1984; but c.f. Bell 1984a and b). The optimal strategy is characterized by

$$\frac{\partial \mu_2}{\partial n} = \frac{S_1 S_2}{t_2} e^{-Ft_1 - Ft_2} \tag{6}$$

under direct costing and

$$\frac{\partial \mu_2}{\partial n} = \frac{S_1}{t_2 S_2} e^{-Ft_1 + Ft_2} \tag{7}$$

under absorption costing (Sibly & Calow, in press). Provided that $\partial\mu_2/(\partial n)$ increases with n (i.e. μ_2 increases increasingly with n) then n_{optimal} increases with

$$\frac{S_1 S_2}{t_2} e^{Ft_1 + Ft_2} \text{ (direct costing)}$$

or

$$\frac{S_1}{t_2 S_2} e^{-Ft_1 + Ft_2} \text{ (absorption costing).}$$

In both cases the optimal strategy is to produce more offspring if juvenile survivorship is higher. The effect of the other parameters depends on whether the costs of reproduction are paid before or after the eggs are laid.

Under direct costing, higher extrinsic adult survival favours more offspring. Slightly lower values of t_2 (which might result from an improved food supply for example) favour more offspring if and only if $-F < 1/(t_2) + \mu_2$ (which is necessarily true in a stable population in which $F = 0$, because $1/(t_2) + \mu_2$ is always greater than zero) (see Appendix 1). Under absorption costing, higher extrinsic adult survival favours *fewer* offspring (i.e. the reverse of the direct costing prediction). Slightly lower values of t_2 favour more offspring if and only if $F < 1/(t_2) - \mu_2$ (Appendix 1). These effects can be combined in a habitat index S; under direct costing,

$$S = \frac{S_1 S_2}{t_2} e^{Ft_1 + Ft_2} \tag{8}$$

while under absorption costing,

$$S = \frac{S_1}{t_2 S_2} e^{-Ft_1 + Ft_2} \tag{9}$$

More offspring should be produced if S is higher (we shall refer to this new result as Prediction 3). It is to be noted, though, that Prediction 3 is very sensitive to the form of the trade-off between μ_2 and n and that though the type of trade-off considered here may be plausible (Calow & Sibly 1983; Calow 1984) it has not been demonstrated beyond doubt in any organism (see also p. 77 and c.f. Bell 1984a and b). More experimental work is urgently needed here. Finally, with regard to Prediction 1 it appears that more matter and energy should be put into reproduction if and only if S is relatively high. Hence, for compatability with Pianka's scheme it is necessary that r-strategies are characterized by high S values, where S is defined by eqns (8) or (9) as appropriate.

It is our view that juvenile mortality rate is likely to be far more sensitive to environmental conditions than that of adults, and if time between breedings is

fixed (as it might be in, e.g. annual breeders) then S would be proportional to S_1. S_1 might therefore turn out to be a useful operational measure of S.

Prediction 2

Initial offspring size will affect time taken to reach first breeding, since if more resources are invested in an offspring initially, fewer remain to be acquired. Thus, other things being equal, bigger offspring would breed earlier, which usually increases fitness (animals which breed once in the season after birth could provide exceptions to this rule; see Sibly & Calow 1983, for further discussion). On the other hand, if offspring are initially bigger, then fewer can be produced from a given quantity of resources. Since, other things being equal, producing fewer offspring decreases fitness, some trade-off has to be made between offspring number and initial offspring size. It turns out that the optimal strategy depends on conditions for individual offspring growth (Sibly & Calow 1982, 1983). If offspring will grow quickly then more, smaller offspring should be produced. The reason is that time to first breeding t_1 is affected both by initial offspring size (Fig. 4.2) and by individual growth rate. If growth conditions are better (as in curve (a) in Fig. 4.2) then offspring will be able to breed earlier (which is why curve (a) is below curve (b). In addition it will take less time to grow from any size X to any other size Y (dotted lines in

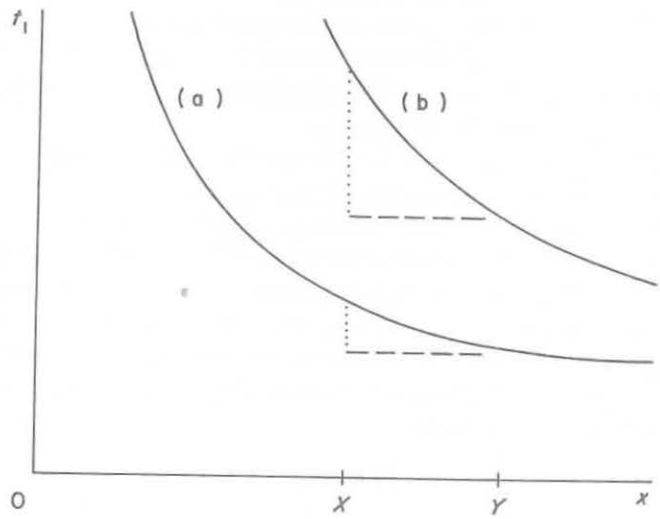

FIG. 4.2. Time to first breeding (t_1) plotted against initial offspring size ($\log_e$ scale), x. Curves (a) and (b) represent good and poor growth conditions for offspring. Dotted lines indicate times taken to grow from size X to size Y. See text for further explanation.

Fig. 4.2), so curve (a) is everywhere shallower than curve (b). (It is assumed that the time taken to grow from size X to size Y is $t_1(X)-t_1(Y)$.) Suppose that the quantity of resources available for reproduction during a particular attempt is Z and that initial offspring size is w, so that $n=Z/w$ (by the 'Principle of Allocation' discussed above). Let $x=\log_e w$. Then from eqn (5)

$$1 = e^{-(F+\mu_1)t_1}\frac{Z}{w}+e^{-(F+\mu_2)t_2} \tag{10}$$

$$\therefore 1 = e^{-(F+\mu_1)t_1+\log_e Z-x}+e^{-(F+\mu_2)t_2} \tag{11}$$

A necessary condition for F to be maximized is that $\partial F/(\partial w)=0$, or equivalently $\partial F/(\partial x)=0$. Differentiating eqn (11) with respect to x and setting $\partial F/(\partial x)=0$ we obtain

$$-(F+\mu_1)\frac{\partial t_1}{\partial x}-1 = 0$$

i.e.

$$\frac{\partial t_1}{\partial x} = -\frac{1}{F+\mu_1} \tag{12}$$

This equation can also be derived from eqn(4) (Sibly & Calow, in press). Hence, the optimal strategy is characterized by a particular slope of curve in Fig. 4.2. Other things being equal, the optimal initial size will be smaller in good growth conditions since curve (a) is shallower than curve (b). The prediction is unaffected by the actual quantity of resources allocated to reproduction, Z, since Z does not feature in eqn (12). Assuming that Z is constant, then, more smaller offspring should be produced in better growth conditions for juveniles (Prediction 4).

This prediction is somewhat sensitive to the values of F and μ_1 (eqn (12)). If F or μ_1 is higher the optimal slope of the $t_1(x)$ curve in Fig. 4.2 is shallower so the optimal strategy is to have fewer larger offspring. Thus, three independent factors favour the production of more, smaller offspring: (i) better growth conditions for the offspring, (ii) lower fitness F, (iii) lower juvenile mortality, μ_1. If these factors vary inversely with one another then the optimal compromise is determined by eqn (12) with reference to the $t_1(x)$ curve.

In assessing growth conditions for offspring in practice it will be necessary to use an index, for example

$$G = \frac{\log_e m(t_b)-\log_e m(t_a)}{t_b-t_a} \tag{13}$$

where t_a is the age at which offspring gain independence, t_b is some slightly later age, and $m(t)$ is offspring mass at age t. An index of this kind is commonly used in assessing plant growth curves (Hunt 1982).

Conclusions

As originally conceived, the theory of r and K selection was framed in terms of the effects of population density but the predictions that can be derived solely on this basis are rather limited (see Introduction). Following the lead of MacArthur, Pianka (1970) constructed a classification of life cycles, in relation to population density, in which high reproductive effort was correlated with producing small offspring. Using the techniques of life-cycle theory we have dissected this relationship into its component parts. Thus, whereas Pianka (1970) maintained that high reproductive effort is selected for by low population density (as in Prediction 1) we now conclude that high reproductive effort is selected for in environments with a high S index (Prediction 3), where S is given by eqns (8) or (9) and is likely to be dependent to a large extent on juvenile survivorship (see above). Predictions 1 and 3 are equivalent if and only if S reduces as population density increases. And whereas Pianka (1970) suggested that the production of fewer larger offspring is selected for by high population density (Prediction 2), we predict that the production of fewer larger offspring is selected for in environments in which juveniles can grow at a slower rate, G (Prediction 4). Predictions 2 and 4 are equivalent if and only if G reduces as population density increases. Furthermore, the correlation of high reproductive effort with the production of small offspring is only to be expected if both S and G reduce as population density increases.

CLASSIFICATION BASED ON THESE LIFE-CYCLE PARAMETERS

One-dimensional classification of selection pressures in terms of density is of limited applicability (Wilbur *et al.* 1974) since density effects are unlikely to operate unimodally on fitness and may have a variety of effects depending upon how they are applied (Boyce, in press). In this paper the focus is shifted away from population density towards two key parameters which directly affect life-cycle strategy; in particular an index S related to offspring survivorship, and an index G indicating rate at which offspring can grow in a habitat. This suggests two- rather than one-dimensional classification. If, for convenience, the two axes, G and S, are divided into high and low the matrix shown in Table 4.1 results. It is now possible to distinguish between four categories of selection: high G, high S; low G, low S; high G, low S; low G, high S. At high S the total investment of resources in reproduction should be high and vice versa at low S. Similarly, at high G propagule size should be small and vive versa at low G. Combining these two predictions, it follows that fecundity

TABLE 4.1. Life-cycle predictions in relation to a dichotomous classification of habitats by G, an index of growth rate of offspring, and S, an index of survivorship defined by eqns (8) or (9) as appropriate. Z = total investment in reproduction during a particular breeding attempt; w = investment per egg; n = number of eggs

G	S: Low	S: High
High	Z low w low n intermediate	Z high w low n very high
Low	Z low w high n low	Z high w high n intermediate

(n) should be highest at high G, high S and lowest at low G, low S, with other habitat types favouring intermediate values. It should be noted, however, that complications may arise if resource availability for adults is higher at high G, with the probable outcome that Z (and hence n) should be increased somewhat in the top row of Table 4.1 (see p. 88). Although strictly one should discuss the two-dimensional G–S continuum it is easier to consider pairwise comparisons and to compare them with the one-dimensional r/K classification, viz:

(1) *Low* S, *low* G *v. High* S, *high* G. This dichotomy is most nearly equivalent to the r/K distinction *as perceived by Pianka* (above) and is referred to by Stearns (1977) as the 'Accepted Scheme'. According to the review by Stearns (1977) the predicted outcome (see Table 4.1) is far from universal, which Stearns took as evidence against r/K selection. However, Pianka's r/K dichotomy is only one possible consequence of density effects and hence the finding that it does not occur is not decisive in refuting their importance (Boyce, in press).

(2) *Low* S, *low* G *v. High* S, *low* G. This represents a gradient in survivorship when conditions for growth are poor. For example, British freshwater triclads all suffer resource limitations (Reynoldson 1983). Yet because of differences in the physiology of hatchlings, the juvenile survivorship of some species is better than others (Calow & Woollhead 1977;

Woollhead & Calow 1979). Absorption costing probably predominates. On this basis, triclads conform well to the predictions since species in which juveniles have good survivorship invest more in reproduction than those that have poor survivorship (Calow & Woollhead 1977; Woollhead & Calow 1979; Woollhead 1983). This kind of gradient in selection pressures is likely to be common in resource-limited top carnivores.

(3) *Low* S, *high* G *v. High* S, *high* G. This represents a gradient in survivorship when conditions for growth are good. For example gyrodactylid ectoparasites (Monogenea) of aquatic vertebrates probably experience good, reasonably stable supplies of food from their hosts, yet different species occupy different sites which differ in vulnerability. Thus, *Gyrodactylus gasterostei* from the skin of three-spined stickleback has higher adult mortality and fecundity than *Gyrodicotylus gallieni* which lives in the more protected site of the mouth of *Xenopus*. Gill parasites probably have intermediate levels of mortality and fecundity. (These data are from P. Harris, cited in Calow 1983.) High growth rates are probably typical of many parasites and so differences in S are likely to play an important part in their life-cycle evolution.

(4) *Low* S, *low* G *v. Low* S, *high* G. This represents a gradient in growth-promoting potential when conditions for survival are poor.

(5) *High* S, *low* G *v. High* S, *high* G. This represents a gradient in growth-promoting potential when conditions for survival are good. Categories (4) and (5) are conveniently treated together for, though there is a considerable amount of information on the way propagule size varies with G, the level of S is rarely specified, probably because G is more readily defined or deduced than S, and it is usually assumed (if only implicitly) that S is constant along gradients of G. G can sometimes be deduced indirectly from environmental variables. Thus, for terrestrial angiosperms seed oil content and weight increase with decreasing illumination (Levin 1974) and there is a tendency for the eggs of marine gastropods to be heavier further offshore where productivity is lower (Rex 1979). G can also be measured directly from individual growth rates. Thus, data from Grime (1979) on annual plants indicate a good negative correlation between growth rate of offspring and log seed weight (Fig. 4.3), and data from Eisenberg (1981) on mammals indicate a good negative correlation between growth rate of offspring and neonatal size (Fig. 4.4). Clearly, care has to be taken in interpreting interspecific comparisons in order not to confuse extrinsic with intrinsic effects and in all these analyses it has to be remembered that correlations do not decisively establish particular causal mechanisms (e.g. S might not be constant). Nevertheless, it is encouraging that all these examples are consistent with Prediction 4, that more smaller offspring are produced in better growth

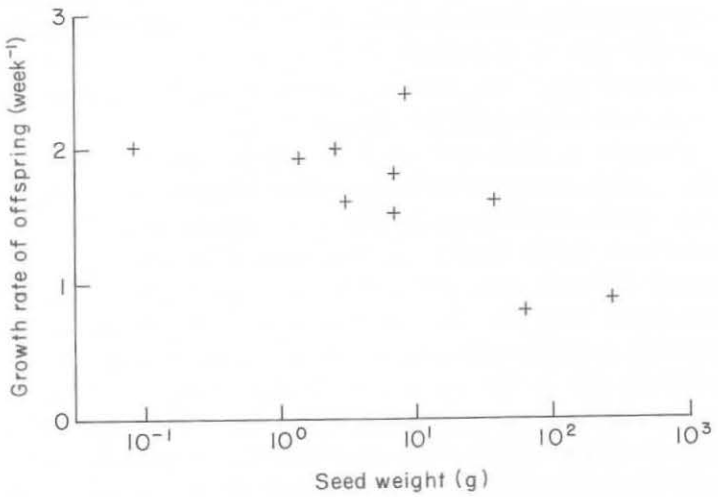

FIG. 4.3. Juvenile growth rate is negatively correlated with log seed weight in ten species of annual competitive-ruderal herbs ($r = -0{\cdot}72$, $P < 0{\cdot}05$). Growth rate estimated as maximum rate of dry matter production per unit weight. Data from Grime (1979, p. 59).

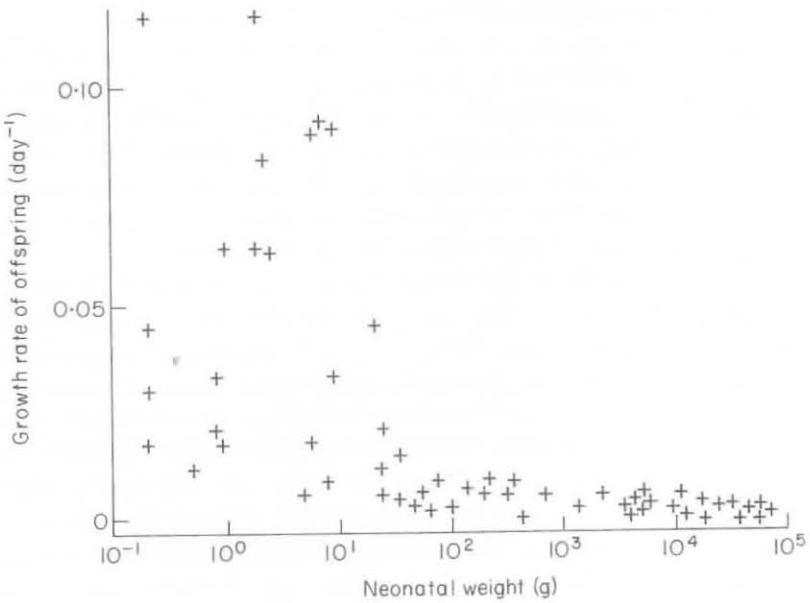

FIG. 4.4. Juvenile growth rate is negatively correlated with log neonatal size in females of fifty-eight species of mammals ($r = -0{\cdot}61$, $P < 0{\cdot}05$). Growth rate estimated as ($\log_e$ (adult weight) $-$ $\log_e$ (neonatal weight))/(age at first mating). (Data from Eisenberg 1981, Appendix 4.)

conditions. Moreover, Ito (1980) has collected together a considerable amount of data on the same topic from a wide variety of sources and taxa and all are generally supportive.

(6) *High* S, *low* G *v. Low* S, *high* G. Here predictions are opposite to the 'Accepted Scheme' (comparison (1), above). It is possible that this distinction applies to endoparasites (which have good conditions for growth, but poor chances of juvenile survival) and free-living relatives (poorer conditions for growth, but better for juvenile survival (Calow 1979, 1983). It is also possibly representative of a general shift in selection pressure with trophic position from the low survival but good growth conditions for herbivores to the higher survival but poorer growth conditions for carnivores (see also Wilbur *et al.* 1974). However, caution is necessary in evaluating this comparison because differences in resource availability could mean that the absolute investment in reproduction at low S high G is equal to or greater than that at high S low G (see pp. 84 and 88).

An axis for disturbance?

In his analysis of vegetative strategies, Grime (1979) distinguishes between two major components of selection pressure—stress and disturbance—and by further distinguishing between high and low levels of each and by noting that no plant can tolerate high levels of both, develops a triangular classification system. Stress is a measure of the extent to which production is inhibited by the environment and hence is the inverse of our G. Disturbance is a measure of the extent to which organisms are killed but represents overall *not* age-specific mortality and so is equivalent to our $-S$ for direct-costing organisms (eqn (8)) but not necessarily for absorption-costing organisms (eqn (9)), for which $S=\exp((F(t_1-t_2))S_1/(S_2t_2)$. In the latter case S varies inversely with disturbance if and only if disturbance affects juvenile more than adult survivorship. For example, if $t_2<t_1$ and disturbance increases both juvenile and adult mortality rates by $\Delta\mu$ then $S_1/S_2 = e^{(\mu_2+\Delta\mu)t_2-(\mu_1+\Delta\mu)t_1} = e^{\mu_2t_2-\mu_1t_1-\Delta\mu(t_1-t_2)}$ which varies inversely with disturbance (however if $t_1>t_2$ the relationship would be reversed, i.e. S increasing as disturbance increases).

The adversity (A) selection of Greenslade (1983) occurs at low G and low *overall* survival. It is likely that mortality falls more heavily on juveniles than adults (hence low S) but this cannot be guaranteed. Hence, the theory can predict that eggs and seeds should be large, but nothing more.

Effects of other variables

Resource availability for adults is one key variable not included in the above analysis. Higher resource availability might mean that individual offspring

could be obtained at lower cost to the adult, e.g. if there were less drain on adult body reserves. This would shift the trade-off curve, $\mu_2(n)$, relating offspring number to adult mortality (p. 79), and the new optimum is likely to involve the production of more offspring (unpublished analysis, see also Calow 1983). If in this case higher resource availability for adults was associated with better growth conditions for offspring, then the effect would be to increase reproductive effort, Z, and fecundity, n, on the top row of Table 4.1, though investment per egg (w) would remain unchanged. Complications for predictions about Z, due to resource availability, may therefore apply where there are gradients in G. When this happens at low S it is likely that Z will not remain constant but will be very low at low G, low S. Similarly, at high S, high G is likely to allow a very high Z and low G a lower Z. These effects accentuate the expected differences in comparison (1) above (low G, low S v. high G, high S), but blur expected differences in comparison (6) (low G high S v. high G low S). In this last instance it is difficult to know a priori whether differences in Z will occur. Comparisons along this axis must therefore be treated with caution. Another possible effect of increased resource availability for adults is a decrease in time between breeding, t_2, which also favours the production of more offspring under some conditions (Appendix 1).

It is also possible to imagine G, S and Disturbance causing evolution of traits that are not currently addressed by life-cycle theory, e.g. capacities for defence, dormancy and dispersal; these kinds of traits are incorporated into the classification tables of Pianka (1970), Southwood (1977), Grime (1979) and Greenslade (1983). Similarly, as well as evoking life-cycle responses, G and S might evoke 'direct' responses. For example, at low G there might be selection for more efficient production and at low S for better survival. In other words, under the influence of evolution, species can shift from one 'square' to another in Table 4.1. Whether and to what extent shifts occur depends on the nature of genetic variance in the population.

It has been assumed here that there are no factors preventing the predicted optima being achieved other than the trade-offs explicitly identified in the models. However, constraints associated with particular taxonomic features, especially size, may be important (Stearns 1984a, b). We would expect the predictions formulated in this paper to be most rigorously tested in comparisons between populations of the same or closely-related species. This is why we urged caution in the interpretations of Figs 4.3 and 4.4.

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APPENDIX 1

Effects of a slight change in t_2 on optimal reproductive effort (Prediction 1)

The effect of a slight change in t_2 can be investigated by differentiating eqns (6) and (7) with respect to t_2. If the derivative with respect to t_2 is positive then increasing t_2 results in an increase in the optimal value of $\partial\mu_2/(\partial n)$ indicating an increase in the optimal value of n, since $\partial\mu_2/(\partial n)$ is assumed to be an increasing function of n. Writing $S_2 = e^{-\mu_2 t_2}$ and differentiating eqn (6) with respect to t_2 we get

$$\frac{\partial}{\partial t_2}\left(\frac{\partial \mu_2}{\partial n}\right) = S_1 e^{-\mu_2 t_2} e^{-Ft_1 - Ft_2}\left(\frac{-\mu_2 - F}{t_2} - \frac{1}{t_2^2}\right)$$

which is negative if and only if $-F-\mu_2 < 1/(t_2)$, i.e. $-F < 1/(t_2)+\mu_2$. Thus, slightly lower values of t_2 favour more offspring if and only if $-F < 1/(t_2)+\mu_2$ for direct-costing organisms.The same method applied to eqn (7) shows that the analogous condition for absorption-costing organisms is $F < 1/(t_2)-\mu_2$.